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The Effects of Litter Quality and Texture on Soil organic Matter Dynamics in Rocky Mountain Soils

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Abstract. We conducted 16 month laboratory incubations of Rocky Mountain forest soils to directly compare the independent effects of plant litter quality and soil texture on soil organic matter (SOM) decomposition and net nitrogen (N) release. We utilized a replicated 2 X 2 design with four possible combinations of texture (high and low clay) and litter quality (high quality aspen and low quality pine). The role of litter quality in plant litter decomposition and N dynamics has been intensively studied, and typically, as litter quality increases so do rates of litter decomposition and N release. In contrast, the role of litter quality in the decomposition of SOM is unexplored for native forest ecosystems. While increased clay content in soil has been related to increased stabilization of SOM, reduced losses of SOM during cultivation, and increased carbon (C) content in younger-age soils, the role of texture in the decomposition of SOM is also not well understood for native forests. Carbon release from incubated soils followed expected general patterns of release: rates were highest at the beginning of the incubation and declined very quickly to a slower rate around month 4. After month 12 there was a second drop to a new base rate. Total CO_2 release (μmoles CO_2/g soil) was highly correlated with soil C content ($R^2 = 0.83$; $P < 0.001$), and including litter type as a second qualitative variable significantly increased the goodness of fit for this regression ($R^2 = 0.94$; $P < 0.003$). Including clay content as a second variable also significantly improved the initial regression's goodness of fit ($R^2 = 0.91$; $P < 0.008$), but in a complete model with soil C and litter type, clay was not significant ($P < 0.184$). Aspen soils consistently released the largest quantities of CO_2, but also contained significantly higher total C than the pine soils ($P < 0.006$). Consequently, over the entire incubation period, pine soils released CO_2 at significantly higher rates (μmoles CO_2/g soil C) than aspen soils ($P < 0.001$). This finding represents a paradox because aspen plant material is of higher quality than pine, suggesting that SOM dynamics are more complex than conceptual models of above-ground litter decomposition would predict. Net N mineralization rates were significantly affected by litter type with aspen soils immobilizing greater quantities of NH_4^+.

Taken together, these results suggest that C and N dynamics of incubated soils reflect both the initial litter quality signature of native SOM and the texture of the soil. Importantly, these effects were not predictable based on current views of organic matter decomposition. Additionally, the interactions of texture and litter quality were significant for some important soil measures suggesting that soil nutrient dynamics in native mixed species systems are more complex than what is observed in single factor studies.

INTRODUCTION

In most terrestrial ecosystems, decomposition of soil organic matter (SOM) is the fundamental process controlling the cycling of nutrients and their availability to plants (Paul et al. 1997; Van Cleve and Powers 1995; Tiessen et al. 1994). Organic carbon (C) in soil can positively influence soil water infiltration capacity, erosion resistance and overall soil quality (Doran et al. 1994). Because organic C can have such profound influences on soil, SOM has been viewed as controlling the functioning of natural and managed ecosystems (Paul 1984). In turn, the accumulation and decomposition of SOM is hypothesized to be controlled by climate, available moisture, litter quality, soil texture, soil mineralogy, nutrient availability, and the composition of soil decomposer communities. Additional importance is ascribed to SOM because soils represent the major pool of terrestrial C (about 1500×10^{15} g: Schlesinger 1977). Controls on the cycling of soil C are therefore central to discussions of global C budgets, especially in the context of climate change.

Melillo et al. (1989) utilized long-term plant litter decomposition data to suggest that organic material is slowly transformed across a "decay continuum" from plant litter to well humified material. These authors presented a conceptual model for litter decomposition in which plant materials of varying quality are decomposed at different rates until the plant materials are reduced to a relatively homogenous "least common denominator" state. The process of homogenization is likened to a decay filter. Before plant material passes across this decay filter, decomposition is controlled by initial litter quality and environmental conditions including temperature, moisture, soil texture, and soil nutrient availability. After plant material passes through the decay filter, decomposition proceeds at a relatively uniform, very slow rate that is controlled by temperature, moisture, soil texture and exogenous sources of labile organic C and nutrients. Alternatively, McClaugherty and Berg (1987) suggest that even in the later stages of forest litter decomposition, decomposition rates are controlled by differences in litter quality that are not filtered out during earlier stages of decomposition. Importantly, because there are few data describing the decomposition of litter that has passed through the "decay filter" into later stages of decay (Aber et al. 1990; McClaugherty and Berg 1987), detailed discussions addressing the dynamics of highly decomposed plant material are lacking.

Nearly all decomposition studies have focused primarily on the transformation of above-ground plant litter into forest floor material (Melillo et al. 1989; Berg 1986; McClaugherty et al. 1985). While the biotic and abiotic factors that control the decomposition of above-ground plant litter have been studied in depth across various litter quality, soil textural, nutrient availability and climate gradients (Scott 1996; Prescott 1995; Vitousek et al. 1994; Aber et al. 1990; McClaugherty

et al. 1985; reviewed by Johnson 1995, Couteaux et al. 1995 and Berg 1986), far fewer studies have addressed the biotic and abiotic factors that control the long-term decomposition of organic matter contained in mineral soil (Scott 1996; Scott et al. 1996; Motavalli et al. 1994; Nadelhoffer et al. 1991).

Nadelhoffer et al. (1991) found that for an Alaskan mineral soil increasing incubation temperatures from 9 to 15°C increased cumulative CO_2 release by about 70%, while increasing incubation temperatures from 3 to 9°C had no effect. In another temperature related study, Winkler et al. (1996) found CO_2 release from incubated soils increased with progressively higher temperatures; however, this effect was short lived and after 20 to 40 days, rates of C release were similar across temperatures. Motavalli et al. (1994) examined the controls of soil mineralogy and texture on mineral SOM decomposition in 13 tropical soils and found that total initial soil organic C was the best predictor of total CO_2 release/g soil during the incubations ($R^2 = 0.83$). Soil clay content was found to be significantly correlated with total C mineralized ($R^2 = -0.44$), but mineralogy had no effect. Scott et al. (1996) examined SOM and litter decomposition in three soils of varying texture, and found that soil texture was directly related to quantities of μmoles CO_2 released/g soil. Because finer textured soils also contained more total organic C, differences among soils in C mineralization rates (μmoles CO_2/g soil C) were much smaller. Finally, Scott (1996) examined the relationship between plant litter quality and decomposition rates for mineral SOM in a series of Wisconsin tree plantations, grass mono-cultures, native forests and planted grassland sites, and found no differences in C mineralization rates among the different vegetation types.

The purpose of the present study is to expand on earlier work and directly compare the effects of initial plant litter quality (substrate source) and soil texture on decomposition rates of mineral SOM and on net nitrogen (N) mineralization rates. We used 16 month laboratory incubations of Rocky Mountain forest soils from sites representing two different plant litter quality types and two soil texture classes, and periodically leached incubated soils of mineral N to test the following hypotheses: 1) soil texture controls C mineralization rates (μmoles CO_2/g soil C) during early and late stages of SOM decomposition because higher clay content soils stabilize greater quantities of organic matter thereby slowing down C mineralization rates; 2) initial plant litter quality controls C mineralization rates during early and late stages of SOM decomposition with higher quality plant litter resulting in higher quality SOM and faster decomposition rates; 3) the microbial community controls C release from soil and differences in the rate of C release will be linearly related to biomass; and, 4) net N mineralization rates will be higher in soils with higher quality substrates (faster decomposition rates) and finer texture (more total substrate).

MATERIALS AND METHODS

Study sites, vegetation and soils

We took advantage of a previous study that characterized N dynamics in 10 lodgepole pine and 10 aspen forests of northern Colorado (Stump and Binkley 1993). Six of the lodgepole pine and 6 of the aspen sites were selected to use for this assessment of litter quality (substrate source) and texture controls on SOM dynamics. The sites were chosen so that they would represent as wide a range in texture as possible. Lodgepole pine (*Pinus contorta* var. *latifolia* Englem.) and aspen (*Populus tremuloides* Michx.) represent two very different forest types. Lodgepole pine is a dominant forest cover type in northern Colorado, with an elevation range from 2,300 m to over 3000 m. Lodgepole pine tends to occur on drier, sandier sites, often in even-aged stands resulting from stand-replacing disturbances. Aspen forests comprise a much smaller percentage of total forest cover in northern Colorado. Aspen occupy a similar elevation range, but tend to occur as patches on wetter, finer textured or on recently disturbed sites. Because pine tends to occur on sandier sites and aspen on finer textured sites, and the effect texture was not part of the previous study, there are 4 aspen clay and 4 pine sand sites, but only 2 stands each of pine clay and aspen sand. The climate in the Colorado Rockies is typified by long cold winters and cool summers. Average annual precipitation for the sites ranged from about 700 mm to 840 mm, with most of this as snow. Consequently, skiing is typically rad.

After removing forest floor, 0-15 cm depth mineral soil was collected from 3 randomly selected points at each of forest sites (Table 1). The soils were transported to lab, stored at 2°C for three weeks until the incubations were started. Prior to incubations, soils were sieved to 2 mm to remove rocks and roots. Each soil was set at field capacity by saturating soils with H_2O on cheese cloth and letting them drain freely for 48 hours. Exactly 50 g (wet weight) of each soil was thoroughly mixed with 40 g acid washed quartz sand, and then placed in micro-lysimeter cups (Nadelhoffer et al. 1991), which in turn were placed in sealable 2 qt mason jars. Twelve laboratory replicates of each soil were incubated for 12 months to gain a better estimate of the mean for each soil type. From months 13 to 16, 3 of the 12 replicates were used because the other 9 became part of another experiment. Base traps were used to absorb the CO_2 evolved from the incubating soils (Anderson 1982). At the end of each incubation month, the base traps were titrated with HCl to determine the quantity of neutralized sodium hydroxide, and respiration estimated.

Soil ammonium (NH_4^+) and nitrate (NO_3^-) pools were initially extracted from a subset of the soils to be incubated by shaking 10 g of sieved soil for one hr with 100 mL of 2 M potassium chloride (KCl) on an Eberbach reciprocating shaker at 180 osc/min, allowed to settle 15 min, filtered through a #42 Whatman filter, and stored frozen (Keeney and Nelson 1982). At

approximately 4 month intervals each of the twelve laboratory replicates (144 soils in all) were leached with 100 mL of dilute nutrient solution (Nadelhoffer et al. 1991) to assess changes in mineral N in the incubating soils and to limit the accumulation of NO_3^- in the soils. At the end of the 16 month incubations, a final KCl extract was performed on the incubated soils to remove any mineral N that had not been removed by the final dilute nutrient leaching at the end of the incubation. Samples were analyzed for $NH_4^+$and NO_3^- on the Lachat Instruments *QuikChem* AE Ion Analyzer according to Lachat Instruments *Quickchem* Methods 12-107-06-2-A (1990) for NH_3 and 12-107-04-1-B (1992) for NO_3^- and NO_2^- . Net N mineralization rates were calculated as the difference between the NH_4^+ plus NO_3 removed in the initial KCL extract, and the cumulative release of $NH_4^+$and NO_3 from the 4 leaching events plus the final KCl extract. Net nitrification rates were calculated as the difference between the initial extracted values of NO_3^- and the NO_3^- removed by the 4 leachings plus the final KCl extract. Percent C and N for each of the soils were determined on a CHN analyzer by dry combustion (LECO-1000). Percent sand, silt and clay and cation exchange capacity were performed by Colorado State University Soil Testing Lab. At the end of the 16 month incubation, the 3 remaining laboratory replicates of the 12 soil types were analyzed by Dr. E.R. Ingham at Oregon State University for total and active fungal biomass and hyphal length, and total and active bacterial biomass.

We held moisture levels and temperature constant throughout the incubations (field capacity ± 5% and 5^oC ± 5%, respectively) in order to isolate the effects of texture and substrate source.

Statistical analyses

Two statistical approaches were used to analyze soil respiration data: the effects of texture and substrate source (factors) on total cumulative CO_2 release and rates (total, labile and recalcitrant) were analyzed by two-way ANOVA, and by simple and multiple linear regression. Cumulative mineral N release and net N mineralization rates were analyzed using one-group and two-group repeated measures, two-way ANOVA, and linear regression analysis. Total C, total fungal biomass and total bacterial biomass comparisons between substrate types were made with two-group t-tests with pooled variance estimates, while microbial data were analyzed using two-way ANOVA, and simple and multiple linear regression (Wilkinson 1996). For all statistical comparisons, $\alpha = 0.05$ was used to determine significance.

RESULTS

Carbon mineralization

During the 16 month laboratory incubations, total quantities of CO_2 released/month ranged from over 120 μmoles CO_2/g soil for the aspen clay soils in the first month of the incubation to less than 10 μmoles CO_2/g soil for the pine sand soils in the last month of the incubation (Fig. 1). All four soil groups lost the largest quantities of CO_2 during the first month of the incubation, after which the quantities of released CO_2 diminished to a baseline level between months 4 and 5. This baseline level was maintained from month 5 to month 12 after which CO_2 release decreased and stabilized at a second baseline level which was maintained to the end of incubation.

Among the four soil groups, there were significant differences in the total quantities of CO_2 released during the 16 month incubations. Clay soils of both litter types released significantly more CO_2 than sand soils (Two-way ANOVA; $P < 0.012$; Fig. 2a). Substrate source did not have a significant effect on CO_2 release/g soil ($P < 0.288$). For these CO_2 comparisons, the interaction of soil texture and substrate source was not significant ($P < 0.514$). When CO_2 release was expressed as μmoles of CO_2/g soil C (to control for initial differences in total soil C) differences among soils due to substrate source were highly significant (Two-way ANOVA; $P < 0.001$; Fig. 2b): pine soils, particularly pine sand, maintained much higher rates of CO_2 release. The statistical significance of the effect of soil texture disappeared when the data were expressed as μmoles CO_2/g soil C ($P < 0.069$), but for the pine soils, lower clay content corresponded to higher rates of CO_2 release. This trend for pine soil is supported by a near significant interaction term for substrate and texture ($P < 0.061$).

Given laboratory conditions, the total quantity of CO_2 released during an incubation of soil represents the most microbially available C contained in that soil. For statistical purposes, we divided our incubations into three time periods (Fig. 1): CO_2 released in the first 4 months, in months 5 through 12, and in the last 4 months were assumed to represent C with fast, intermediate, and slow release, respectively. These divisions potentially belie the gradient nature of soil C quality, but they permitted an assessment of the effects of soil texture and substrate source on the C released during the first and last periods. An estimated average monthly release of CO_2 for months 5 to 16 was not subtracted from total monthly releases for the first four months because it is yet to be established that SOM can be divided into pools (Parton et al 1995), and if they can, how decomposition rates for a slow or intermediate pool changes in the presence or absence of a readily available C source.

The quantity of labile C released was much larger than the quantity of slow C released (Fig. 3a and b). Clay soils released significantly more labile C (μmoles CO_2/g soil) than sand soils (Two-way ANOVA; $P < 0.037$), while the effect of substrate source and texture by

substrate interactions were not significant ($P < 0.824$ and $P < 0.491$, respectively). When labile C release was expressed as μmoles CO_2/g soil C (Fig. 3c), the effect of substrate source was highly significant ($P < 0.002$), while the effect of texture was non-significant ($P < 0.080$); again texture by substrate interactions were not significant ($P < 0.079$). Clay soils also released significantly more slow C (μmoles CO_2/g soil) than sand soils ($P < 0.037$), while the effect of substrate source was insignificant ($P < 0.123$). When slow C release was expressed as μmoles CO_2/g soil C (Fig. 3d), the effect of substrate source was significant ($P < 0.044$), while the effect of texture was no longer significant ($P < 0.599$). Interactions for both comparisons were not significant ($P < 0.966$ and $P < 0.554$, respectfully).

Carbon to N ratio is often used as an index of organic matter quality (Paul and Clark 1996; Parnas 1976) especially in litter decomposition studies. However when C:N of the soils were plotted against total CO_2 release or C mineralization rates, no relationships emerged and using C:N as a second variable did not improve goodness of fit for the above regression ($P < 0.516$).

Nitrogen mineralization

Rates of cumulative total NH_4-N release during the 16 month incubations varied from just above 0 μg N/g soil N for both aspen soils to about 7 μg N/g soil N for the pine sand (Fig. 4a). For each of the four leachings, pine soils consistently released more NH_4-N/g soil N. Repeated measures analysis of the cumulative release curves revealed that substrate source significantly effected the total cumulative release of NH_4-N ($P < 0.020$). Two-way ANOVA analysis of total NH_4-N released after 16 months also revealed that the effect of substrate source was significant ($P < 0.007$). A significant leaching event by substrate source interaction ($P < 0.002$) in the repeated measures analysis indicated that rates of NH_4-N released (slopes of the fits to cumulative release curves) were also larger for pine soils. Neither the effect of soil texture nor the interaction of texture and substrate source were significant ($P < 0.599$ and $P < 0.726$, respectively).

Patterns of release for total NO_3-N were different than release patterns for NH_4-N (Fig. 4b), but no statistical differences (two-way ANOVA or two-group repeated measures) were found for the effects of either soil texture or substrate source. Overall, sand soils did appear to release more NO_3-N than clay soils. One-group repeated measures analysis revealed that the pattern of NO_3-N release for aspen clay soils was significantly different from the other three soil groups ($P < 0.001$).

Aspen soils had significantly larger initial 2M KCl extractable NH_4-N pools than the pine soils (*P < 0.043*: *data not shown*): mean pool size for the aspen soils was 17.9 μg N/g soil, while for pine soils, mean size of the initial pool was 8.7 μg N/g soil. Soil texture did not appear to have any influence on the size of initial NH_4 pool, and neither substrate source nor texture influenced the final extractable NH_4 pool size. Soil texture and substrate source had no effect on the quantity of initial extractable NO_3 (*P < 0.926* and *P < 0.171*, respectively). When these KCl extract data were expressed as μg N/g soil N, there were no significant effects of soil texture or substrate source on either the initial NH_4 or NO_3 pools. For total final extractable pools (representing both the total quantities of either NH_4 or NO_3 leached during the incubations plus the quantities of NH_4 or NO_3 removed during the final 2M KCl extraction), the only significant effect was that of substrate source on the NH_4 pool, expressed either as μg N/g soil or μg N/g soil N (*P < 0.001* and *P < 0.021*, respectively).

Net rates of N mineralization (change in measured mineral N levels) were comparable to, but slightly less than net nitrification rates (change in measured NO_3-N levels) for all soils (Fig. 5a and b). Net mineralization rates (μg N/g soil N) were significantly effected by substrate source (*P < 0.043*), while net nitrification showed a non-significant trend with substrate. In both cases pine soils consistently released larger net quantities of mineral N/ g soil N than the aspen soils.

Microbial Biomass

There were large differences among soil groups for the microbial measures taken (Fig. 6). Soil texture significantly affected active (*P < 0.049*) and total (*P < 0.043*) bacterial biomass, with clay soils supporting higher biomass. Pine clay soils supported significantly more active fungal biomass and total active biomass (*P < 0.001* for both) than the other soil groups, which did not differ significantly. Active fungal length was also significantly greater in pine clay than the other three soil groups (*P < 0.005: data not shown*). Total fungal biomass, representing > 97% of the total microbial biomass, was significantly higher in Aspen clay soils than in the other three soil groups (P < 0.034).

DISCUSSION

Carbon mineralization

We found that total initial soil C was the best predictor of total CO_2 released (Fig. 7a: R^2 = 0.83, *P < 0.001*) and total final soil C was the best predictor of slow C release (Fig. 7b: R^2 = 0.83, *P < 0.001*). Scott (1996), in a study of tree plantations, planted grasslands and grass

mono-cultures, and Motavalli et al. (1994) in a study of tropical forest soils, both found that the best predictor of total CO_2 release was total initial soil C. From ANOVA analyses, texture was significantly related to the total quantity of CO_2 released from soil. The significance of this effect reflects the high level of correlation between soil clay content and total soil C (Fig. 8a): given the correlation between initial soil C and CO_2 release, the significance of clay-CO_2 release relationship is not surprising (Fig. 8b). However, the lack of a texture effect when CO_2 release is expressed on a rate basis (μmoles CO_2/g soil C), particularly for aspen soils, contradicts our hypothesis regarding texture to C mineralization rates (Fig. 8c).

In contrast to Scott (1996), we found that substrate source did significantly effect C dynamics.

If data for a Wisconsin oak loam soil (Scott 1996) and a Pacific northwest loam soil (Hart et al. 1994) are included with our data, the regression for total soil C versus CO_2 release is improved ($R^2 = 0.87$). By including these two additional sites, the regression line represents a strikingly wide range of forest types, climatic conditions, soil mineralogies, soil textures, and incubation temperatures (5, 21 and 25°C!). Motavalli et al. (1994) found that mineralogy did not significantly effect patterns of C release from their tropical forest soils: as with our study clay content was correlated with CO_2 release. The apparent lack of a temperature effect is difficult to explain because it suggests that temperature does not influence the decomposition rate of SOM. If the SOM had responded to temperature as normally predicted (i.e. a Q_{10} of 2; Raich and Schlesinger 1992), then the Wisconsin and Oregon soils should have released 3 to 4 times the quantity of CO_2 per unit of soil C. Interestingly, Motavalli et al. (1994) and Muamba (1991) found rates of release for their tropical soils, which were incubated at > 30°C, to be similar to rates present here.

Other studies have also found somewhat anomalous relationships between temperature and decomposition rates of SOM. In a forest soil heating experiment, Peterjohn et al. (1993) found that elevating soil temperatures in the field by 5°C for 316 d resulted in a large loss of forest floor mass compared to unheated controls, but no loss of C from mineral soil. Winkler et al. (1996) found that after day 20 of a long-term soil incubation, initial differences in rate of CO_2 release for 15 and 22°C trials disappeared: release rates were nearly identical from days to 20 to 120 and by the end of the incubation, the 15°C trial had lost 87% of the C as the 22°C trial. Nadelhoffer et al. (1991) examined temperature controls on the decomposition of an Alaskan mineral soil and found that if incubation temperatures were increased from 9 to 15°C cumulative CO_2 release after 13 weeks increased by about 70%, but if incubation temperatures were increased from 3 to 9°C, CO_2 release did not change. The controls of temperature on SOM dynamics in forests are not well understood and warrant further study.

Linear regression analysis indicated that significantly larger quantities of C were contained in aspen soil per unit of clay (Fig. 8a), and that clay content was correlated with μmoles CO_2 released/g soil (Fig. 8b: $R^2 = 0.81$; $P < 0.001$). Including clay content as a second variable in the regression between soil C and CO_2 release (Fig. 7a) significantly improved the goodness of fit for this relationship ($R^2 = 0.91$; $P < 0.016$). The relationship of soil clay content with total soil C and C mineralization rates provides some evidence for why pine soils maintained higher rates of C release/g soil C than the aspen. For pine soils, C mineralization rates increased (non-significantly) with decreasing clay content (Fig. 8c), a trend that did not exist for aspen soils. In addition, aspen soils maintained overall lower C mineralization rates than pine soils per unit of clay, in part explaining why aspen sites accumulated more soil C per unit of soil clay (Fig. 8a). Therefore, the high correlation between clay content and CO_2 release can be viewed as the balance of more C per unit clay but lower C mineralization rates per unit C in aspen versus pine soils.

While these results lend support to the ANOVA results and to previous findings that texture can influence C dynamics by stabilizing SOM (Sorenson 1981; Oades et al. 1989; Oades 1984), substituting substrate source (a 2 level qualitative variable) for clay as a second variable resulted in a better model for the linear relationship between total soil C and CO_2 release ($R^2 = 0.94$; $P < 0.003$). The aspen sites mostly fell below this regression line, while the pine sites generally fell above the regression line, indicating that litter type may integrate both texture and litter quality variables. Importantly, in a regression model that included all three variables, clay was not significant ($P < 0.184$). The interactions of texture, litter quality soil C (and probably plant production) complicate interpretations and suggest that texture can influence soil SOM dynamics both directly (through stabilization of SOM) and indirectly (through changes in vegetation).

The aspen soils contained higher C than texturally similar pine soils, and substrate source very significantly influenced C mass loss rates (Fig. 2b). However, the slope of the regression line (0.599) and the high degree of association for total soil C and total CO_2 release (Fig. 7a) indicates that C mineralization rates decreased linearly with linear increases in total soil C. This suggests that the proportion of labile C to total C in soil is inversely related to total organic matter content which supports the finding that C mineralization rates were significantly higher for pine soils than for aspen soils (contrary to our hypothesis). Rates of total mass loss ranged from about 10% for the aspen soils to 16% for pine clay soils and 27% for the pine sand soils. Previous estimates of litter quality at our sites (N content; C:N, cellulose content, lignin:N; rates of mass loss for leaf and root material) demonstrated that both below and above-ground

aspen plant material from our sites was of higher quality than pine plant material (Stump and Binkley 1993). Because initial above-ground litter quality has been shown to be an important control on litter decomposition (Melillo et al. 1989; McClaugherty and Berg 1987; Berg 1986), the much higher rates of C release for pine versus aspen soils represent somewhat of a paradox.

The simplest explanation for this paradox is that aspen litter somehow is not of as high a quality as the pine litter. While every index of plant litter quality was consistently higher for leaves and roots of aspen (aspen roots and leaves even decomposed more quickly than pine during a 6 month incubation), aspen roots contained more total lignin at the two sites where root lignin was measured (224 mg/g root vs 214 for pine; Stump and Binkley 1993). If these data represent a real (albeit small) difference between aspen and pine roots, and below-ground production in aspen is equal to or greater than at the pine sites, then increased inputs of this decay resistant material (~2% of the total root mass) may explain why aspen soils released less CO_2/g soil C, and accumulated more but mineralized less C per unit of clay. The production assumption is reasonable because: 1) pines growing in finer textured soils were much more productive than similar aged pine growing in sandier soils (Stump and Binkley 1993); 2) aspen generally occupy wetter, finer textured sites; and 3) aspen soils had higher concentrations of exchangeable and total nutrients (Table 1).

If the SOM under aspen is of a lower quality than pine SOM, then the decomposer community under pine should be better able to utilize pine SOM than the aspen decomposer community can utilize aspen SOM, i.e. the microbial community should be more efficient at converting SOM into biomass under pine. This idea is supported by the observation that aspen soils generally contained more organic matter than pine soils (i.e. the gap between C gained by inputs of fresh material C and lost to decomposition is larger in aspen than in pine soils) (Table 1). If the aspen soil decomposer community is adapted to inputs of relatively high quality plant material but decomposes only a portion of this material, then over time the lowest quality "left-overs" accumulate. Because CO_2 release/g soil C was higher in pine than in aspen soils, a microbially-based litter quality explanation is reasonable.

Total bacterial biomass was positively correlated with slow soil C (Fig. 9a; $R^2 = 0.59$; $P < 0.003$) with a doubling of soil C corresponding to about a 30% increase in bacterial biomass for both pine and aspen. For fungal biomass, a doubling of soil C corresponded to no increase in fungal biomass for pine but a quadrupling in fungal biomass for aspen (Fig. 9b). Total fungal biomass was also correlated with total soil C (Fig. 9b; $R^2 = 0.58$; $P < 0.004$), and significantly improved the fit of the relationship between total bacterial biomass and CO_2 release (Fig. 10a;

$R^2 = 0.91$; $P < 0.001$). Because a two-fold increase in soil C corresponded to a 50% increase in slow CO_2 release, the release of CO_2/ug of microbial biomass varied across the C gradient represented by the 12 incubated soils. The much larger biomass of fungi compared to bacteria (from 40:1 to 200:1) suggests that most of the soil respiration measured was from fungi, despite the significant relationship between bacterial biomass and CO_2 release (Fig. 10a). Finally, because fungi are more effective at decomposing recalcitrant organic material like lignin (Paul and Clark 1996), the high ratio of fungi to bacteria at the end of the incubation suggests that soil communities had shifted in response to a declining labile C supply.

Across the low end of our soil C gradient, a doubling of fungal biomass corresponded to about an 80% increase in CO_2 release (Fig. 10b). If microbial efficiency = microbial biomass C / (biomass C + CO_2 respired) (as used by Hart et al. 1994), and the assumption is made that C content in microbial biomass does not vary significantly among the soils, then microbial efficiency did not appear to be clearly related to texture or substrate source (Fig. 10a,b): two of the aspen clay sites were the most efficient while one of the pine clay sites was the least. However, because the ratio of bacteria to fungi was inversely correlated with microbial efficiency (i.e. as the ratio favored more fungi, microbial efficiency increased; Fig. 11: $R^2 = -0.76$; $P < 0.001$), microbial efficiency (and therefore apparent substrate quality) may have more to do with the decomposer community than with the substrates. Microbial efficiency does not provide information about the mean residence time for microbial C, and changes in microbial efficiency may not correspond to changes in mean residence time.

This aspen-pine paradox points to a complication regarding assessments of or efforts to model SOM decomposition in forests. The size of the organic matter pool in soil is controlled by the net balance of production inputs and losses due to decomposition. Therefore, SOM quality should be controlled by the extent to which inputs of material are processed and the rate at which these processed materials accumulate. Because organic matter processing depends on climate, litter content of decay resistant compounds, the soil decomposer community, texture, and the interactions of these variables, linear increases in the C balance of production and decomposition may be non-linearly or even inversely related to the relative quality of the accumulating SOM. Initial plant litter quality, particularly leaf litter quality, is likely to be an overall poor predictor of SOM quality and decomposition rates. For the most part, controls on organic matter decomposition have been investigated in mass loss experiments with fresh litter. Results from these studies are difficult to extrapolate to mineral soils in forests without more data on root production, the turnover and relative quality of SOM, and a more detailed understanding of how mineral soil interacts with plant material as it decomposes.

Interestingly, the rates of SOM mass loss were comparable to rates for intact above-ground litter (Aber et al. 1990; Melillo et al. 1989), indicating that either the soil environment is better suited for the decomposition of organic material or that mineral SOM is as decomposable as fresh plant litter. Evidence in support of the first explanation is mixed (Scott et al. 1996; Holland and Coleman 1987; Cogle et al. 1987; McClaugherty et al. 1985). Because substrate source significantly influenced C mineralization rates for the labile (Fig. 3a,c) and slow C (Fig. 3b,d), substrate source influenced patterns of release for all of the C respired during our 16 month incubations. There are two possible interpretations: either our soils had not passed through the decay filter of Melillo et al. (1989) or substrate source ultimately affects the decomposition of even the most recalcitrant C fractions in soil (McClaugherty and Berg 1987). Melillo et al. (1989) did not observe a stabilization in mass loss until about month 28 of their decomposition study: because we ended our incubations after 16 months and given the similarity between rates of mass loss for SOM and litter, either interpretation is plausible.

Nitrogen mineralization

The N leaching and extract data for our soils indicated that there were significant N cycling differences among soils (Fig. 5,12), particularly in the way the different soil groups responded to declining C supply (Fig. 4). Stump and Binkley (1993) found that rates of net N mineralization (area basis) were higher overall in the soil and forest floor of aspen than lodgepole pine forests. In the present study, when rates were corrected for initial N differences, net N mineralization rates (N/g soil N) decreased significantly along a gradient of increasing soil N (Fig. 5b, 12b). These findings do not contradict the findings of Stump and Binkley (1993), because in their study, soils were the dominant source of N mineralized and aspen soils contained more total N than pine.

Hart et al. (1994) used long-term (456-d) incubations to elucidate C controls on N cycling in a mineral soil from the H.J. Andrews Experimental Forest in central Oregon. They found that gross nitrification rates were high throughout the incubation but NO_3^- immobilization rates declined as substrate quality or availability declined. The end result was a large net release of NO_3^- after 140 d. In the present study, an increase in the net release of NO_3^- was observed after 120 days for the two sand soils and after 240 d for the pine clay soil. The aspen clay soils had not undergone a large increase in the size of the NO_3^- pool through day 480 of the incubation, suggesting that the net balance of mineralization and immobilization was small in these high clay, high C soils. The quantity of N leached (Fig. 4), the net quantities of N mineralized and nitrified (Fig. 5, 12), the patterns of C release from soil (Fig. 1), and a strong

inverse relationship between total CO_2 release and net rates of N mineralization (Fig. 14) indicate that N supply was coupled to soil C dynamics, as suggested by Hart et al. (1994). These authors found highly significant relationships between gross N mineralization or immobilization rates and total CO_2 release ($R^2 = 0.97$ and $R^2 = 0.98$, respectively), and suggested that soil respiration may be a useful index of N cycling. If these relationships hold for our soils, then it is possible that total initial soil C, substrate source and soil texture influenced gross N process rates for the 12 soil types. Hart et al. (1994) cautioned that the relationship between microbial respiration and gross N process rates may be unique to each soil type and to specific laboratory conditions. In our study, soil types did vary, but sampling and laboratory conditions were consistent across soil types. Further, because a net release of NO_3^- indicated a decline in gross rates of NO_3^- immobilization and therefore a decline in C supply, the relationship between net N release and CO_2 release (Fig. 14) suggests that increased immobilization (i.e. microbial activity as defined by CO_2 flux) limited the release of NO_3^-, the dominant N form released duringour incubations.

CONCLUSIONS

The results from this study indicate that controls on SOM dynamics differ substantially from those of above ground litter. Texture provided an important control on the efflux of total, labile and slow CO_2-C from soil, but contrary to our hypothesis, texture did not significantly affect absolute rates of C mineralization. For our soils, the role of texture in SOM decomposition is most likely related to the relationship between texture and C storage, which reflects the balance of both production and decomposition. Substrate source did significantly effect C mineralization rates, but contrary to our hypothesis, aspen SOM decomposed at a lower rate than pine SOM. While initial differences in the total quantity of lignin in the roots of these two species may explain these findings, the mechanisms responsible for this paradox are not clear. We did find important microbial differences among soils that may have confounded insights into why aspen SOM was lost at slower rates than pine SOM: microbial efficiency was inversely related to the ratio of bacteria to fungi, and fungi are known to be more efficient at decomposing recalcitrant material. Therefore, differences in substrate quality that could be reflected in microbial efficiency, are masked by differences in microbial community structure that inturn reflect those substrate quality differences. Importantly, two different microbial communities with similar efficiencies may differ in mean turnover times for C that could directly affect the quantity of C processed by a given quantity of biomass. Nitrogen dynamics were also

difficult to predict from initial information about litter quality: after correcting for initial differences in soil N content, net rates of N release were higher for pine soils. We did find surprisingly good relationships between clay content and total soil C, and total soil C and CO_2 release. Importantly, the effect of clay content on soil C mineralization and storage was species specific. Our results confirm previous suspicions that we know less about forest SOM dynamics than we think.

Table 1

Location	Forest Type	Elevation (m)	Stand age	pH	Texture	%clay	%C	%N	C:N	Total P
Roosevelt NF	Populus tremuloides	2740	70	6.03	Clay loam	31.0	6.3	0.350	18.0	650
Fraser Exp. For	Populus tremuloides	2820	80	5.97	Clay	39.0	9.4	0.460	20.4	858
Routt NF	Populus tremuloides	2730	95	6.20	Loam	19.0	5.3	0.440	12.0	760
Arapaho NF	Populus tremuloides	2800	70	5.97	Sandy clay loam	18.0	7.7	0.420	18.3	769
Fraser Exp. For	Populus tremuloides	2800	40	6.53	Sandy loam	17.0	4.7	0.250	18.8	670
Fraser Exp. For	Populus tremuloides	2830	90	5.87	Sandy loam	9.0	3.2	0.190	16.8	577
Routt NF	Pinus contorta	2960	65	4.97	Clay loam	32.0	4.7	0.230	20.4	500
Roosevelt NF	Pinus contorta	3210	90	5.20	Loam	19.0	2.7	0.130	20.8	350
Routt NF	Pinus contorta	2870	160	4.87	Loam	11.0	1.1	0.090	12.2	135
Fraser Exp. For	Pinus contorta	2830	70	5.37	Sandy loam	11.0	1.8	0.080	22.5	343
Fraser Exp. For	Pinus contorta	2800	70	5.53	Sandy loam	11.0	1.4	0.110	12.7	443
Roosevelt NF	Pinus contorta	2920	250	5.57	Sandy loam	7.0	1.7	0.090	18.9	226

Figure 1

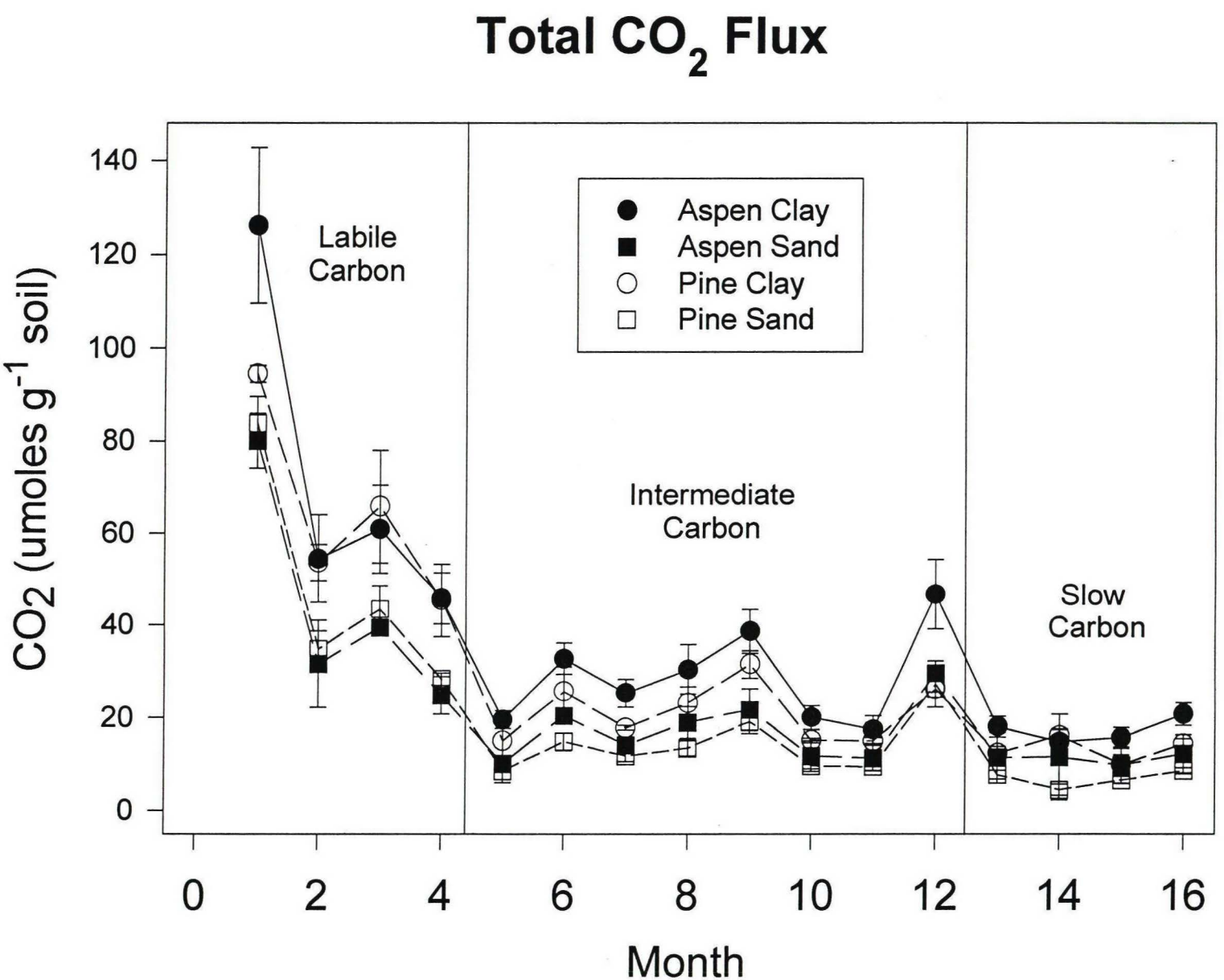

Total CO_2 Flux
CO_2 (umoles g^{-1} soil)
140
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
Month
Labile Carbon
Intermediate Carbon
Slow Carbon
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand

Figure 2

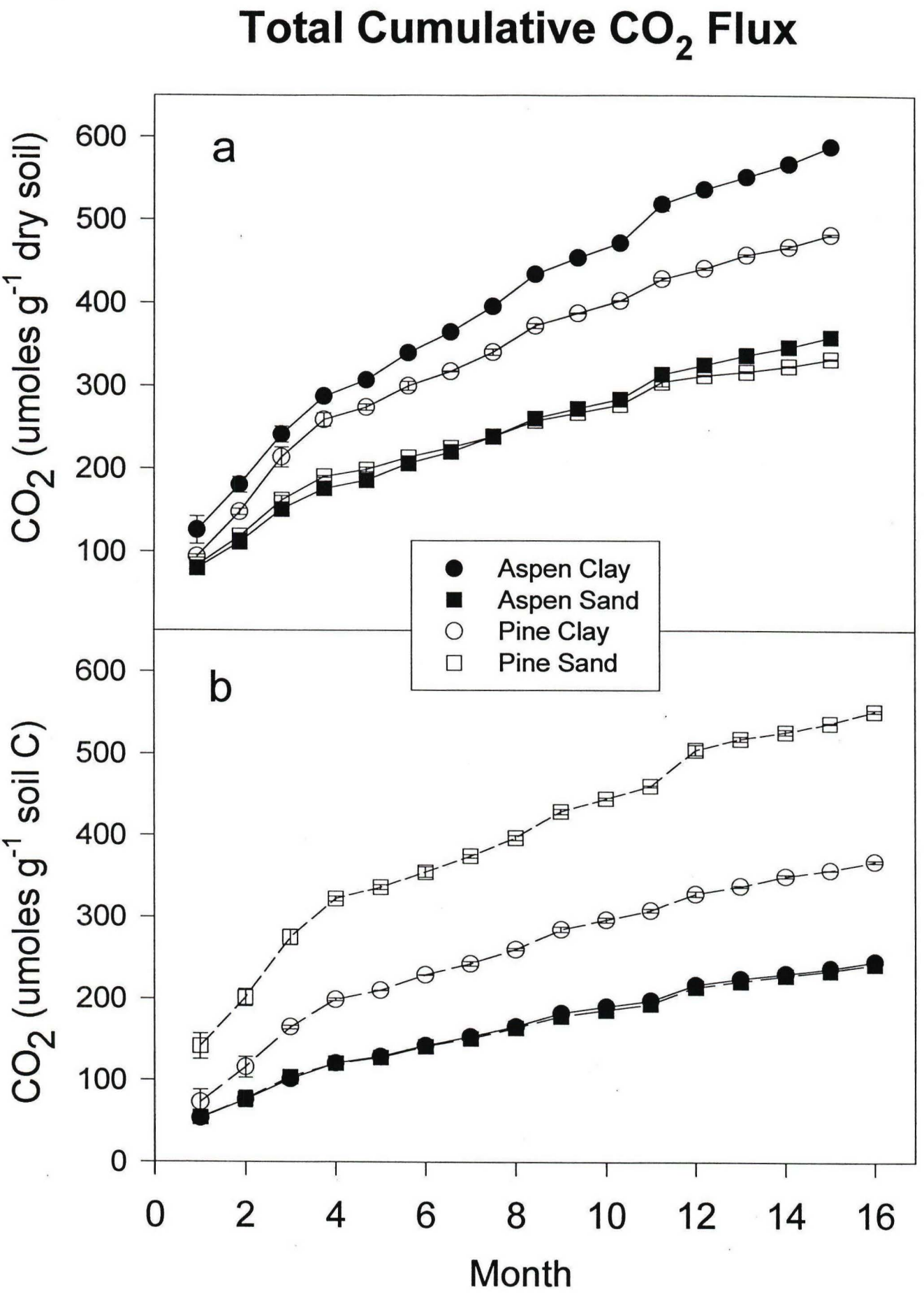

Total Cumulative CO_2 Flux
a
b
CO_2 (umoles g^{-1} dry soil)
CO_2 (umoles g^{-1} soil C)
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
0
100
200
300
400
500
600
0
2
4
6
8
10
12
14
16
Month

Figure 3

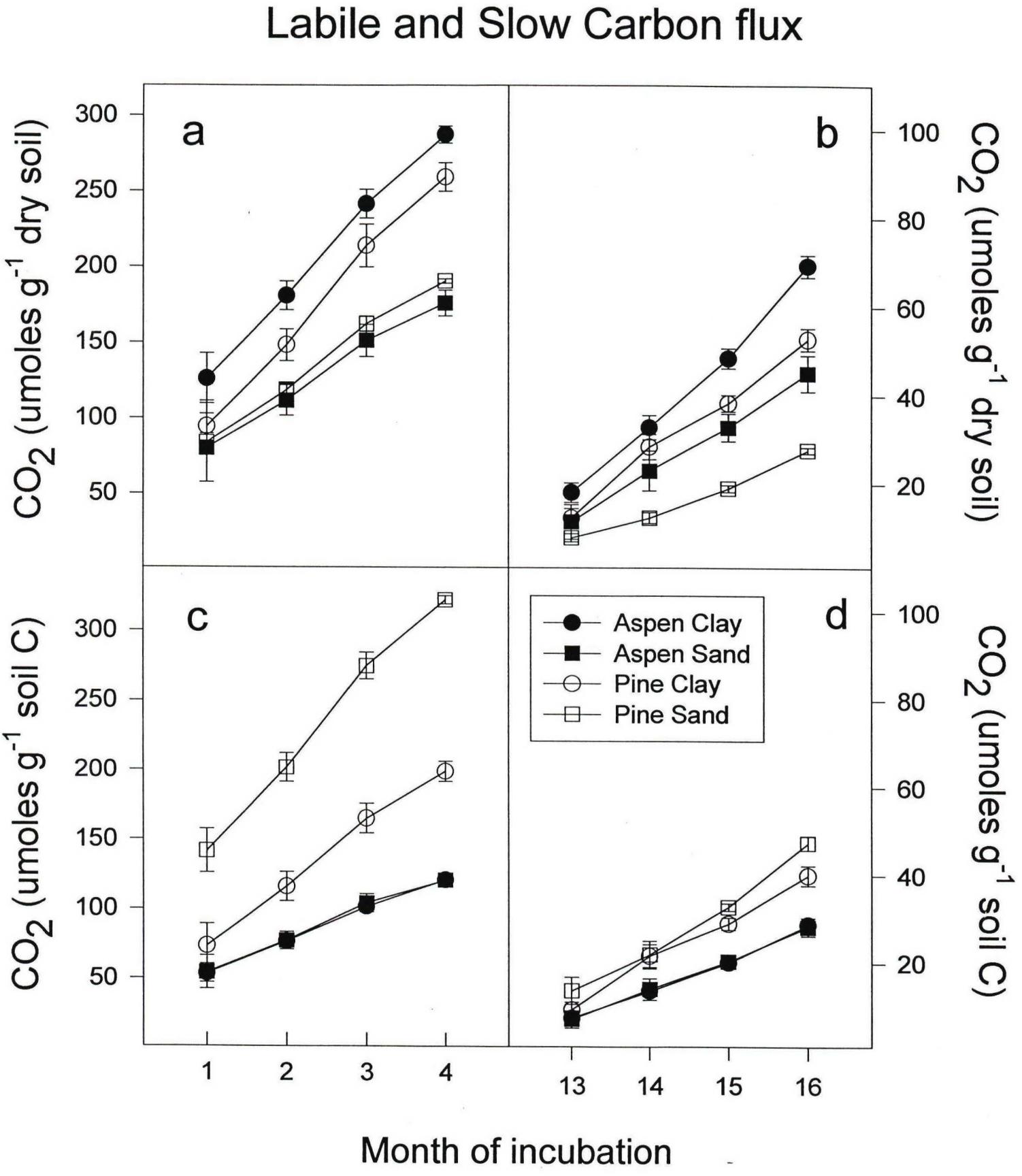

Labile and Slow Carbon flux
a
b
c
d
CO_2 (umoles g^{-1} dry soil)
CO_2 (umoles g^{-1} soil C)
300
250
200
150
100
50
100
80
60
40
20
1
2
3
4
13
14
15
16
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
Month of incubation

Figure 4

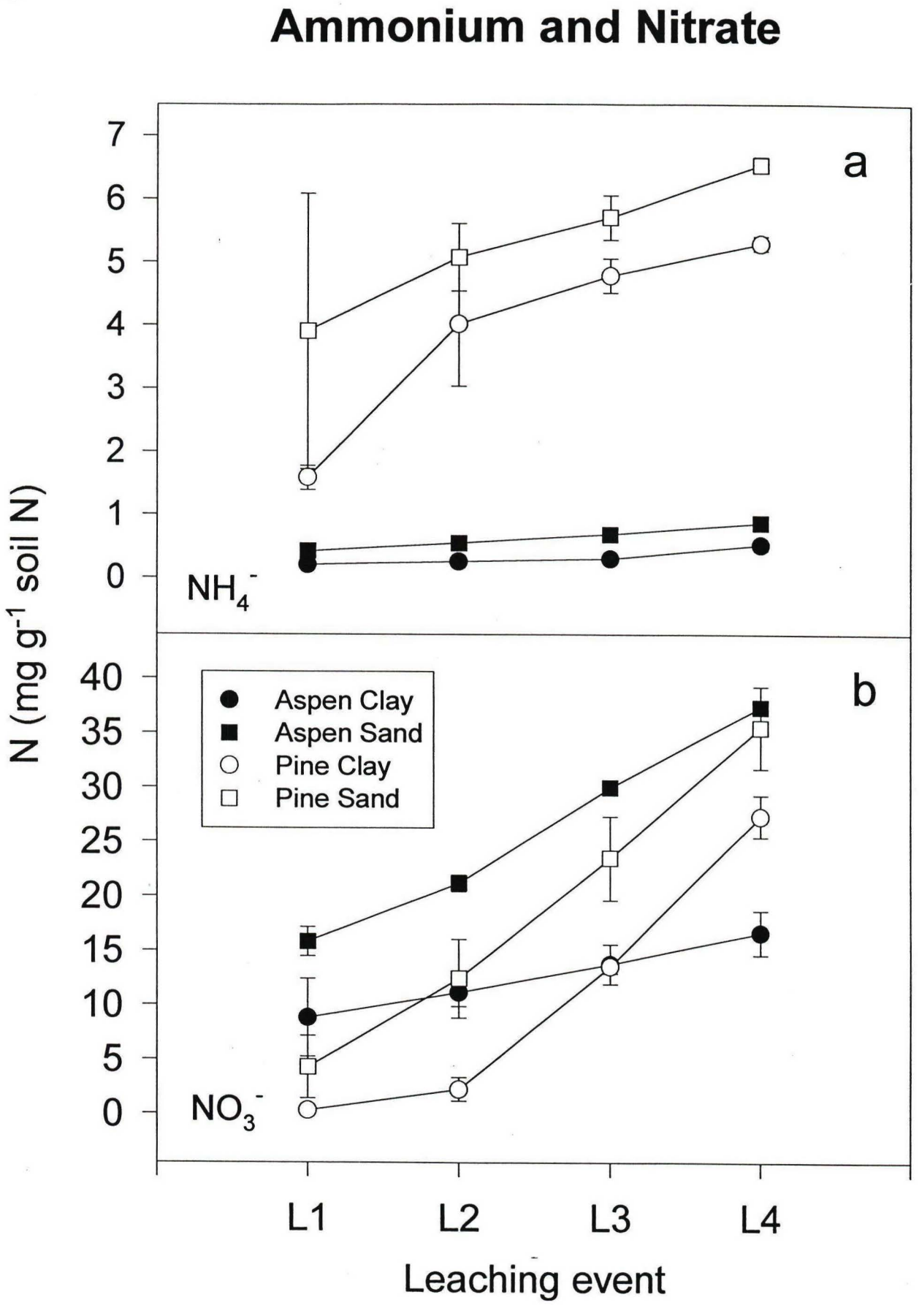

Ammonium and Nitrate
a
b
NH_4^-
NO_3^-
N (mg g^{-1} soil N)
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
L1
L2
L3
L4
Leaching event

Figure 5

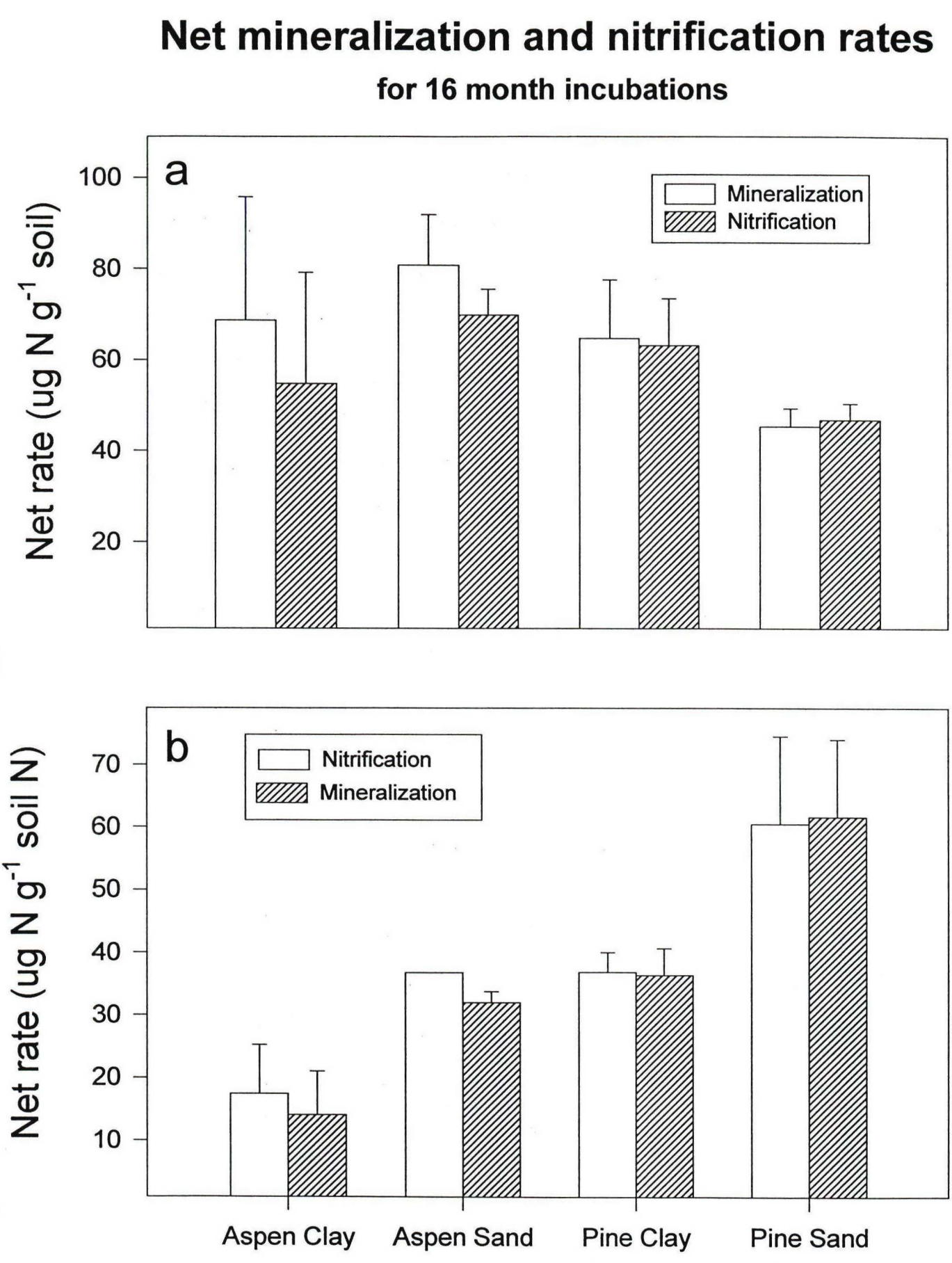

Net mineralization and nitrification rates
for 16 month incubations
a
Mineralization
Nitrification
Net rate (ug N g-1 soil)
100
80
60
40
20
b
Nitrification
Mineralization
Net rate (ug N g-1 soil N)
70
60
50
40
30
20
10
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand

Figure 6

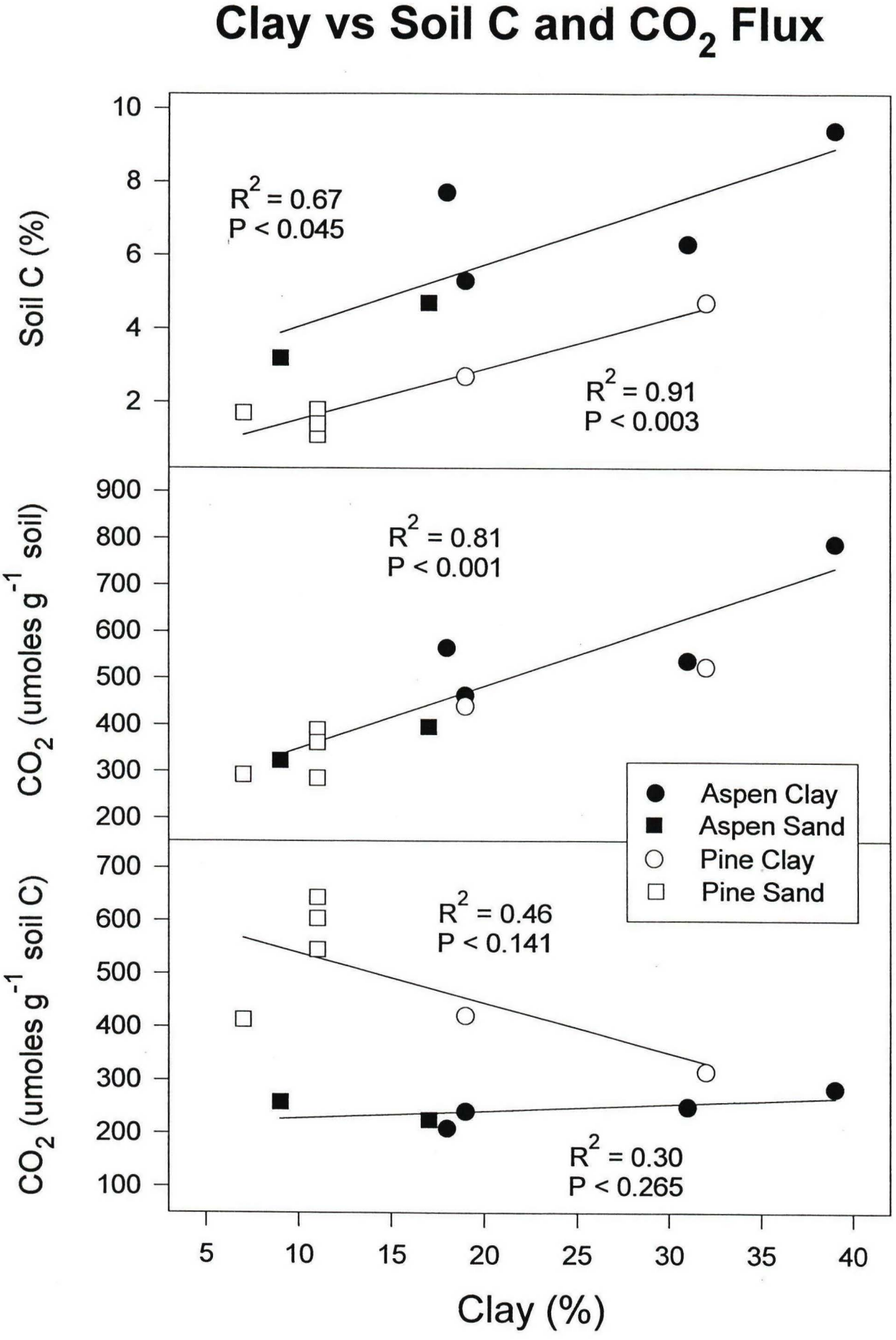

Clay vs Soil C and CO_2 Flux
Soil C (%)
R^2 = 0.67
P < 0.045
R^2 = 0.91
P < 0.003
CO_2 (umoles g^{-1} soil)
R^2 = 0.81
P < 0.001
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
CO_2 (umoles g^{-1} soil C)
R^2 = 0.46
P < 0.141
R^2 = 0.30
P < 0.265
Clay (%)

Figure 7

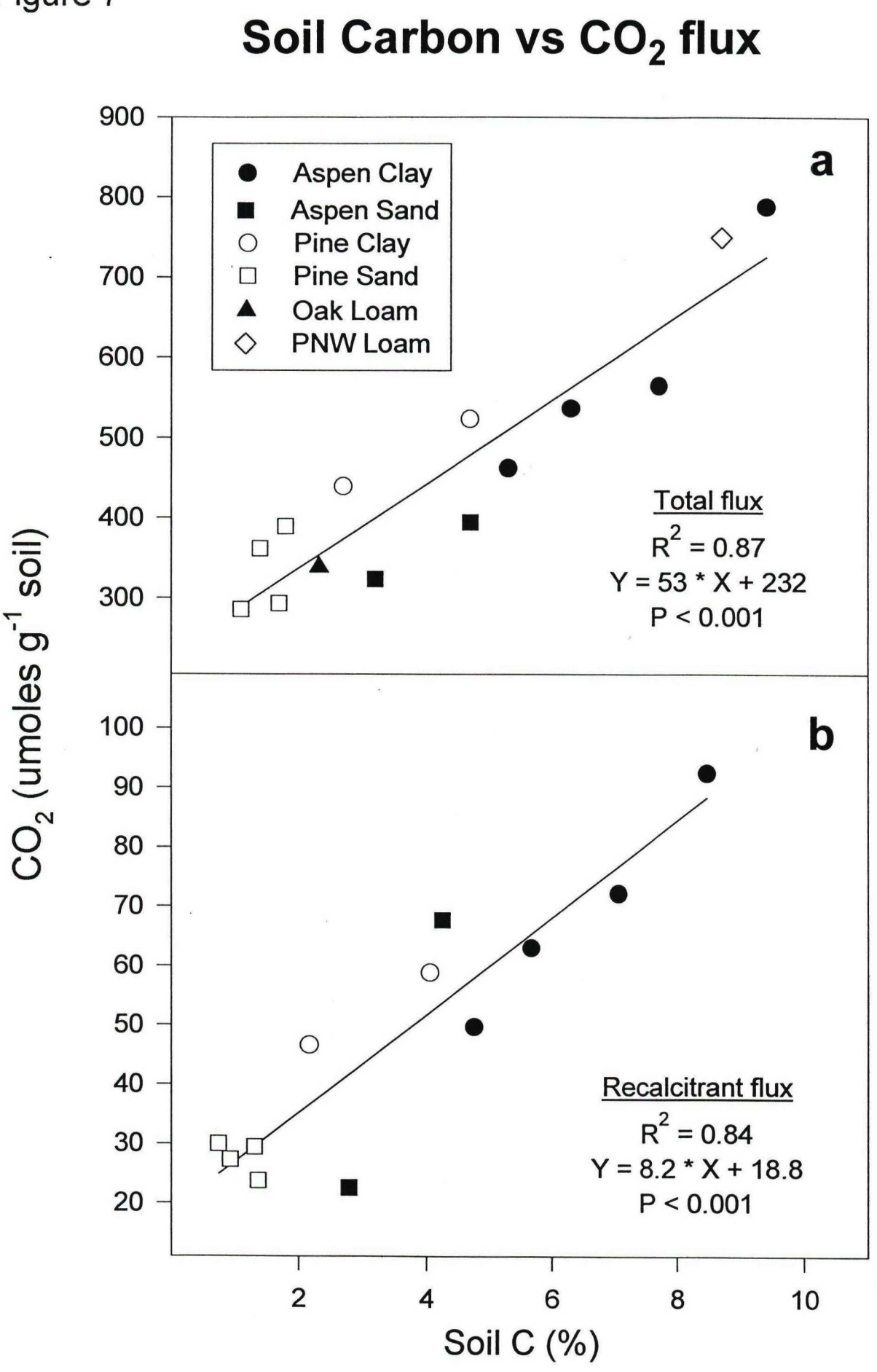

Soil Carbon vs CO_2 flux
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
Oak Loam
PNW Loam
a
Total flux
R^2 = 0.87
Y = 53 * X + 232
P < 0.001
b
Recalcitrant flux
R^2 = 0.84
Y = 8.2 * X + 18.8
P < 0.001
CO_2 (umoles g^{-1} soil)
Soil C (%)
900
800
700
600
500
400
300
100
90
80
70
60
50
40
30
20
2
4
6
8
10

Figure 8

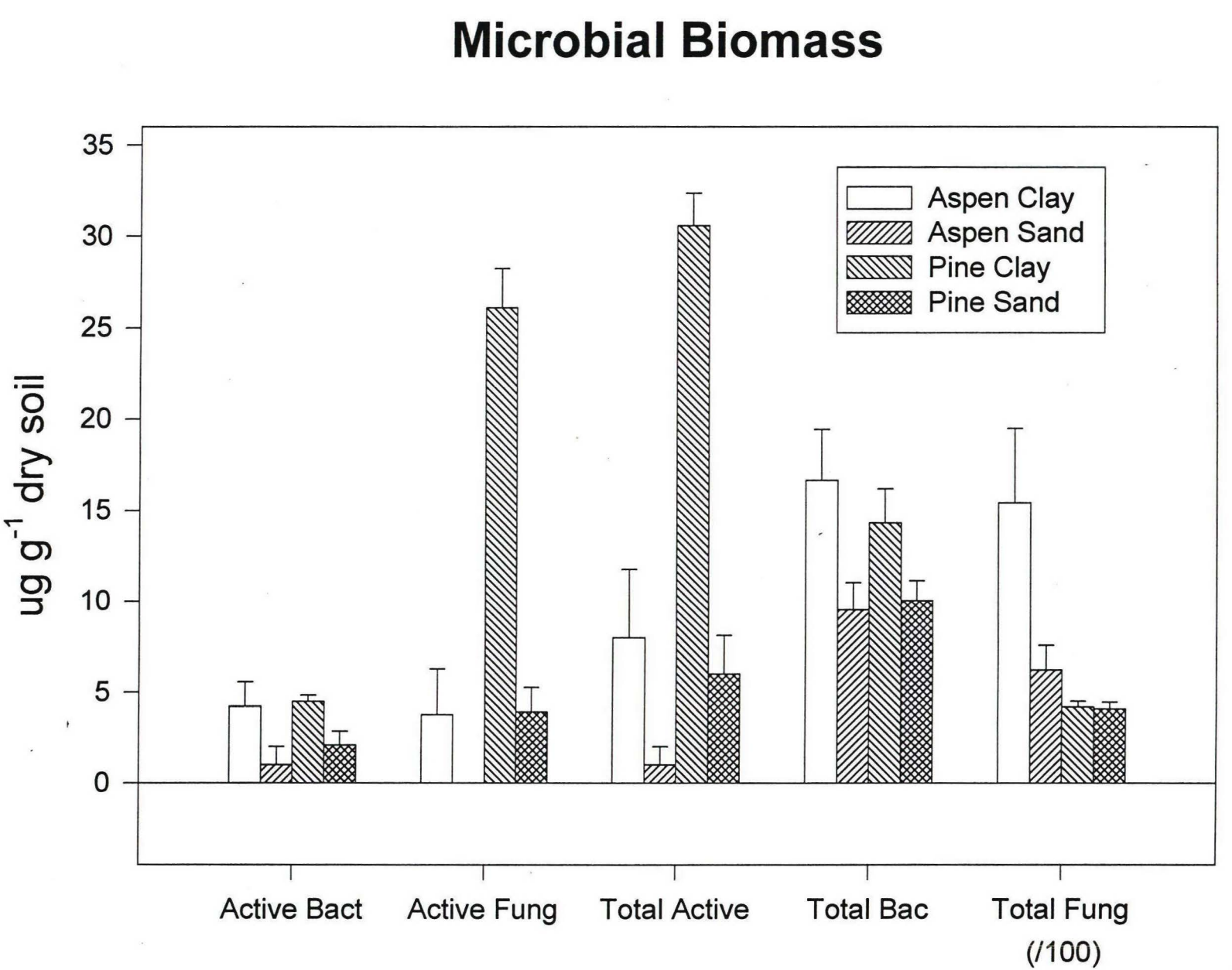

Microbial Biomass
ug g-1 dry soil
35
30
25
20
15
10
5
0
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
Active Bact
Active Fung
Total Active
Total Bac
Total Fung
(/100)

Figure 9

Soil Carbon vs. Microbial Biomass

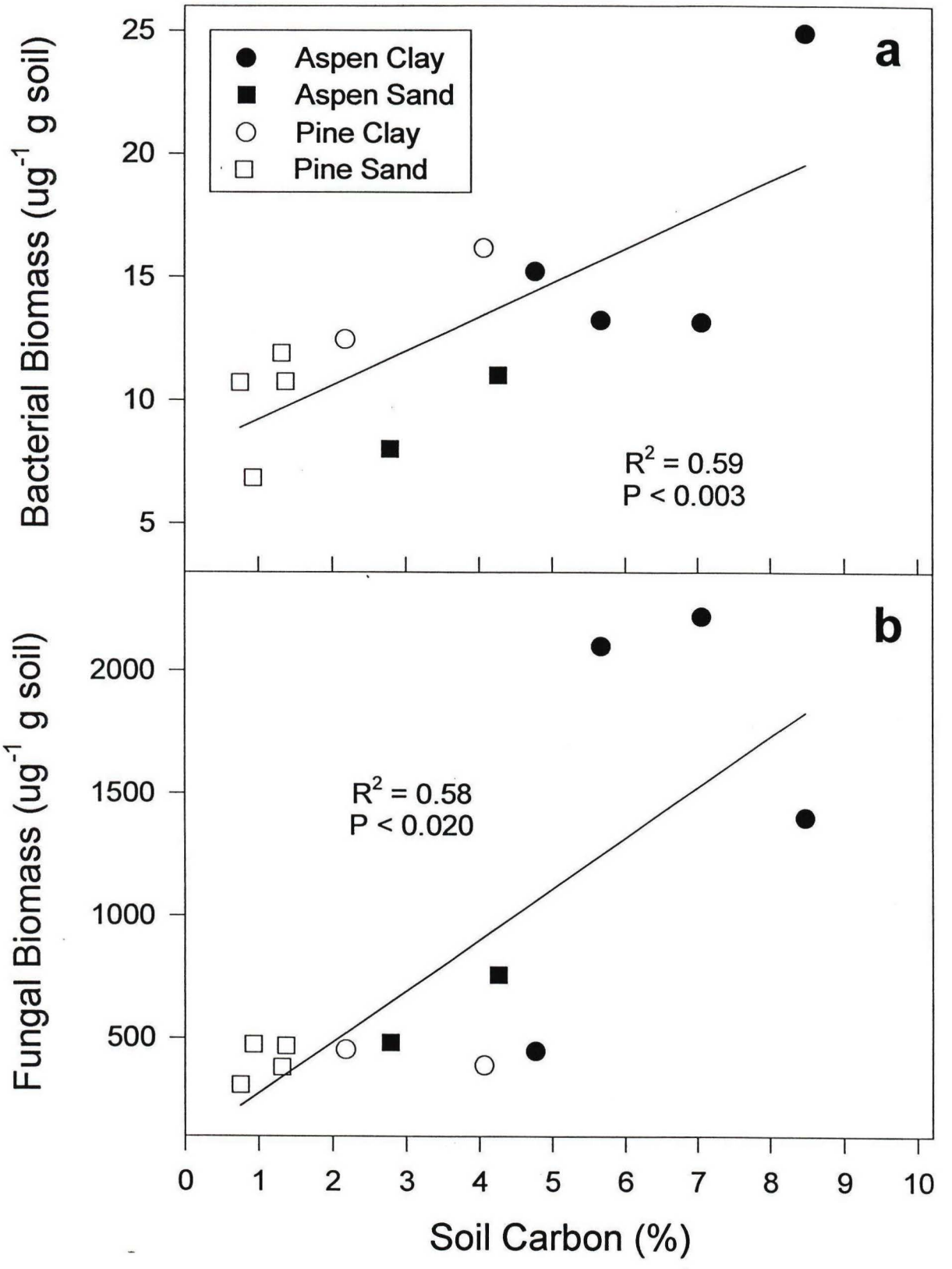


Figure 10

Microbial Biomass vs Recalcitrant CO_2 release

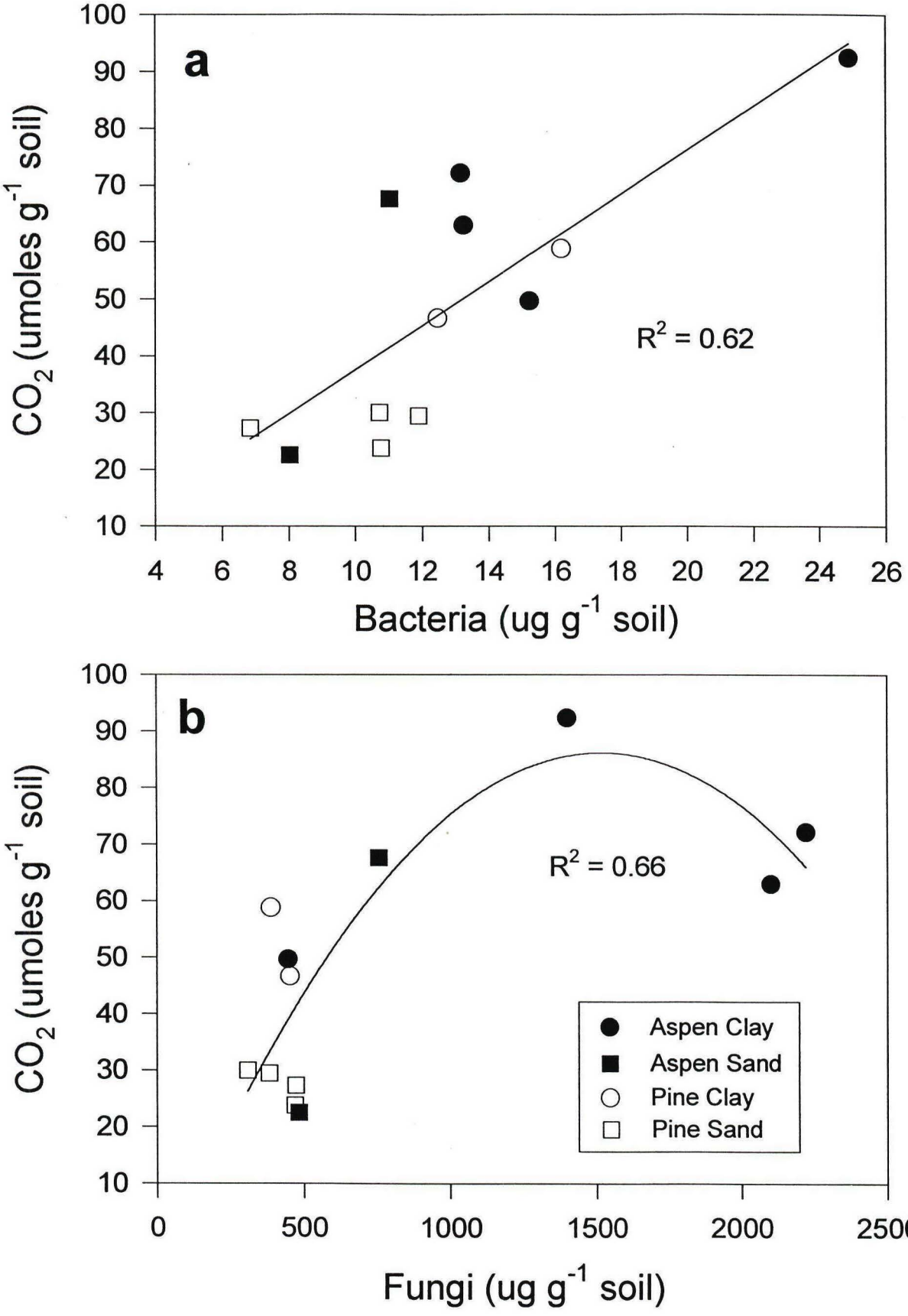


Figure 11

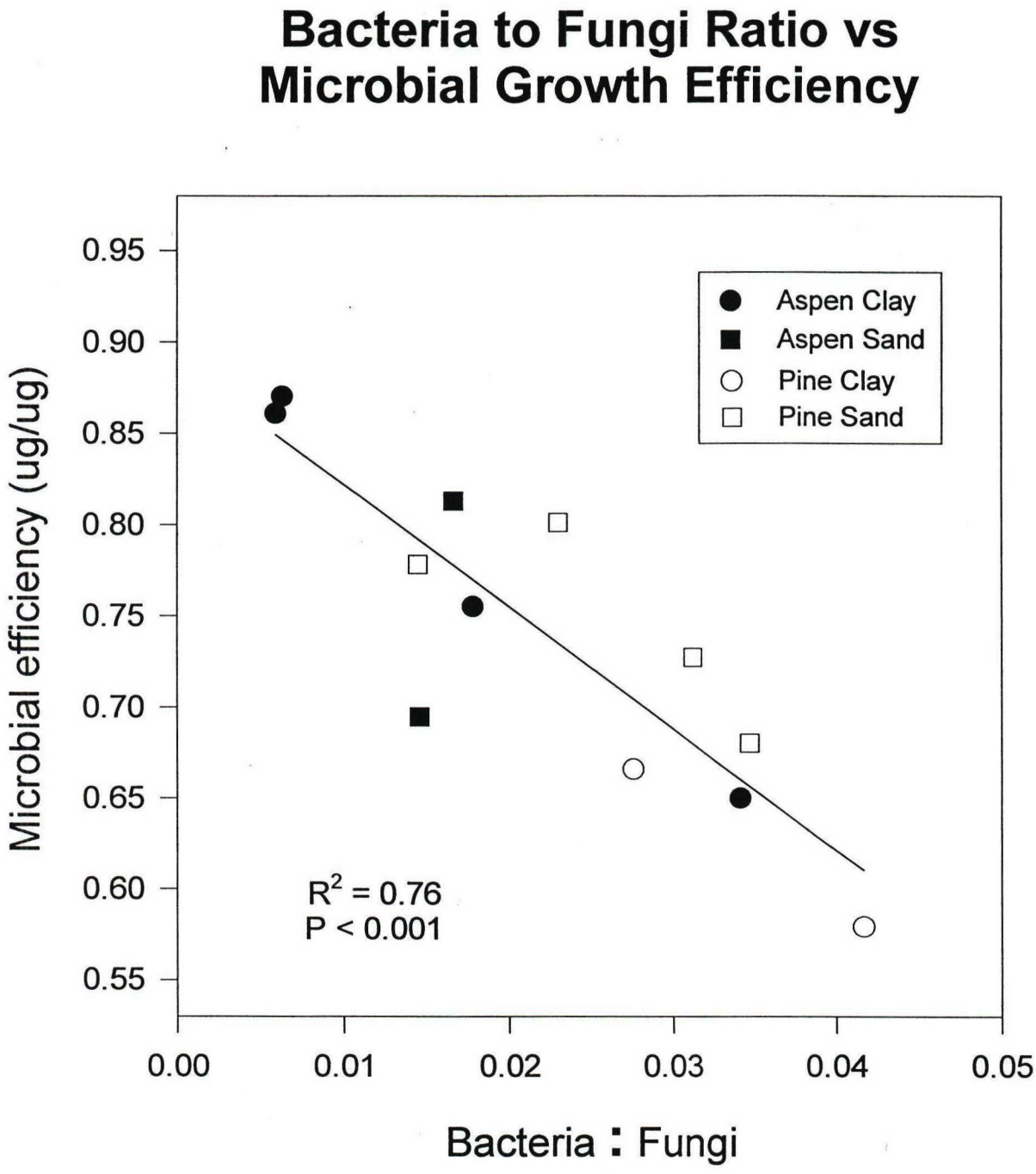

Bacteria to Fungi Ratio vs
Microbial Growth Efficiency
Microbial efficiency (ug/ug)
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.00
0.01
0.02
0.03
0.04
0.05
Bacteria : Fungi
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
R2 = 0.76
P < 0.001

Figure 12

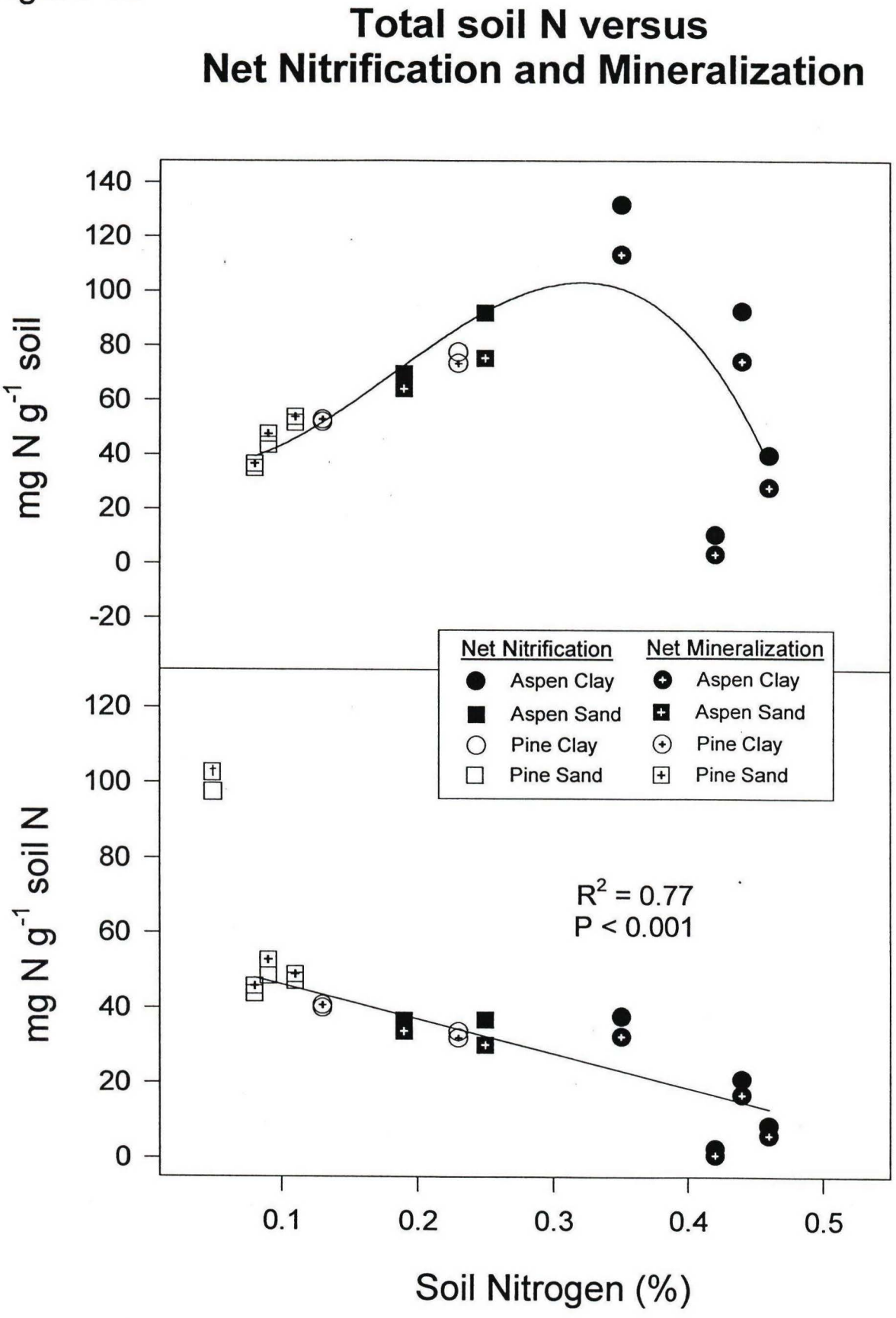
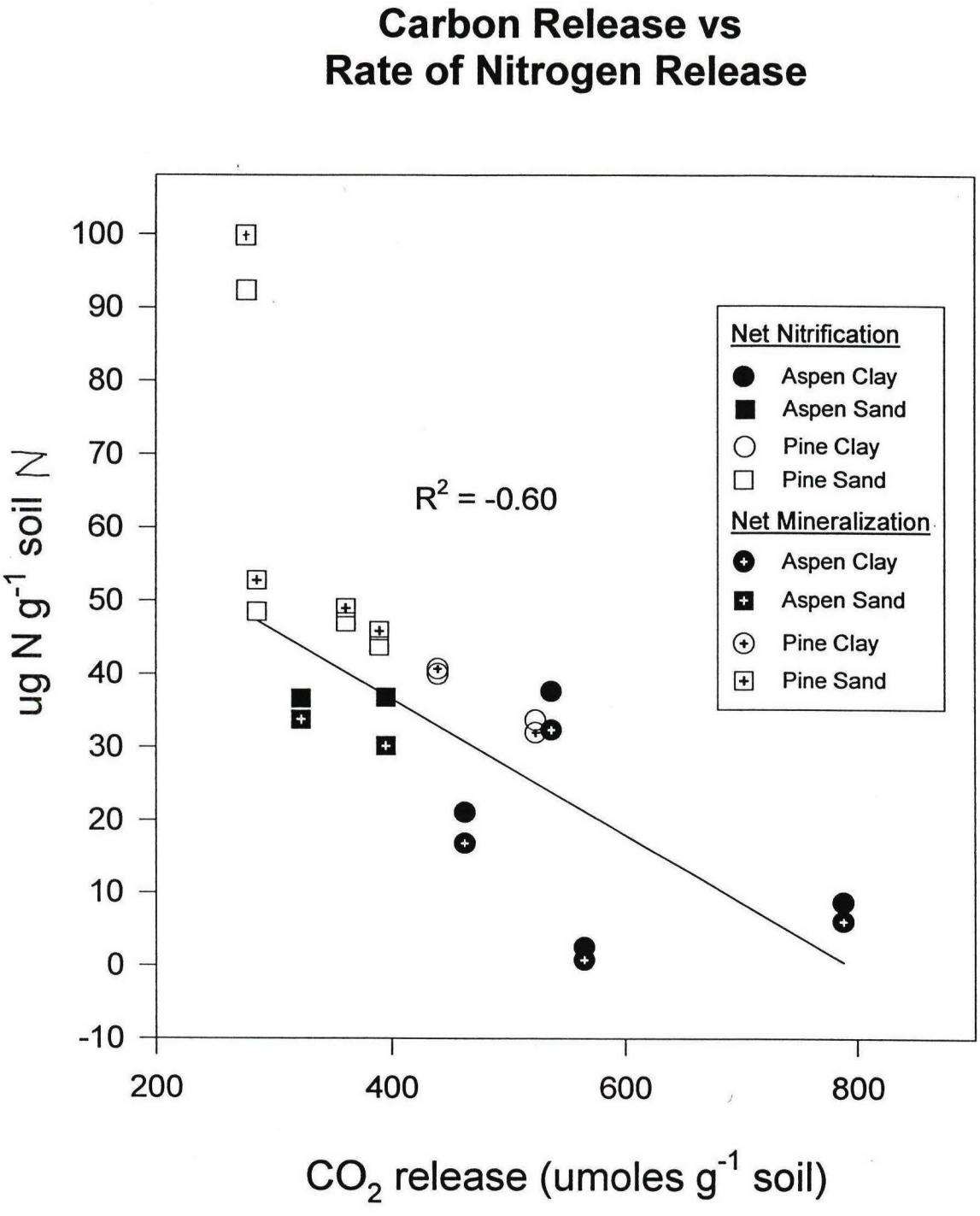

Total soil N versus
Net Nitrification and Mineralization
mg N g-1 soil
mg N g-1 soil N
Net Nitrification
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
Net Mineralization
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
R2 = 0.77
P < 0.001
Soil Nitrogen (%)

Figure 14


Carbon Release vs
Rate of Nitrogen Release
ug N g-1 soil N
100
90
80
70
60
50
40
30
20
10
0
-10
200
400
600
800
CO2 release (umoles g-1 soil)
R2 = -0.60
Net Nitrification
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand
Net Mineralization
Aspen Clay
Aspen Sand
Pine Clay
Pine Sand